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COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENiaceae, I. WOOD ANATOMY

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THE TAXONOMIC TREATMENT of the Dilleniaceae has been based, for the most part, on a limited number of characteristics which are not well defined nor thoroughly understood. As a result, a survey of the taxonomic literature reveals that there is little agreement on the proper phylogenetic position of the family (TABLE 1). This taxon has been included in as many as six orders and allied to no less than fifteen different families. Not only is there considerable controversy regarding its position in relation to other families, but there is still no satisfactory treatment to show intrafamilial relationships.

The early placement of the Dilleniaceae was in association with the ranalian complex, e.g., by Bentham and Hooker (1862) who divided the seventeen genera recognized by them as comprising the taxon into three tribes, based mainly on the form of the stamens. It is also interesting to note that these workers recognized the putative affinity of *Crossosoma* to the Dilleniaceae. Such an affinity was to be argued for many years.

On the basis of the supposed parietal placentation, Gilg (1893) in Engler and Prantl's *Die natürlichen Pflanzenfamilien*, placed the family between the Sterculiaceae and Eucryphiaceae in his large order Parietales. The artificiality of this order has been noted by Lawrence (1951) and by Standley and Williams (1961); their arguments have been supported by anatomical evidence described by T. K. Wilson (1960, 1964, 1965, 1966) in connection with his investigations on the Canellaceae. Within the family Gilg formed three subfamilies and six tribes and included the genera *Actinidia* and *Saurauia*. In a later edition of the *Syllabus*, Gilg and Werdermann (1925) removed the two above-mentioned genera to form a separate family Actinidiaceae. The four tribes within the Dilleniaceae proper were retained.

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TABLE 1. — Systematic Treatment of the Dilleniaceae

AUTHOR	PLACEMENT
DE CANDOLLE, 1824	Ranales; between Ranunculaceae and Magnoliaceae
LINDLEY, 1830	Ranales; between Magnoliaceae and Winteraceae
BENTHAM & HOOKER, 1862	Ranales; between Ranunculaceae and Calycanthaceae
BAILLON, 1871	between Ranunculaceae and Magnoliaceae
LE MAOUT & DECAISNE, 1873	Ranales; between Ranunculaceae and Calycanthaceae
KUNTZE, 1891	between Ranunculaceae and Calycanthaceae
GILG, 1893	Parietales; between Sterculiaceae and Eucryphiaceae
HALLIER, 1905	Rosales; near Brunelliaceae
WARMING, 1911	Cistiflorae; near Bixaceae
BESSEY, 1915	Ranales; between Ceratophyllaceae and Canellaceae
GILG & WERDERMANN, 1925	Parietales; near Actinidiaceae
RENDLE, 1925	Guttiferales; near Ochnaceae
HUTCHINSON, 1926	Dilleniales; near Connaraceae
WETTSTEIN, 1935	Guttiferales; near Actinidiaceae
GUNDERSEN, 1950	Theales; near Actinidiaceae
LAWRENCE, 1951	Parietales; near Actinidiaceae
TAKHTAJIAN, 1958	Theales; near Actinidiaceae
BOIVIN, 1956	Dilleniales; near Crossosomataceae
BENSON, 1957	Ranales; between Annonaceae and Cercidiphyllaceae
COPELAND, 1957	Guttiferales; near Theaceae
CRONQUIST, 1957	Dilleniales; near Crossosomataceae
CHADEFAUD & EMBERGER, 1960	Parietales; near Actinidiaceae
EAMES, 1961	Dilleniales; near Paeoniaceae
MELCHIOR, 1964	Guttiferales; near Paeoniaceae

Hoogland (1952, 1953) suggested the family should be divided into two subfamilies, the Tetraceroideae and Dillenioideae, again based primarily on stamen morphology. According to this author, the genera within the Dillenioideae show reticulate relationships with their arrangement depending on the principles employed.

At the present time, the most widely accepted treatment places the Dilleniaceae, Paeoniaceae, and Crossosomataceae in close alliance under the Dilleniales (Eames, 1961). Cronquist (1957, 1965) noted, however, that this association was not firmly established and suggested, furthermore, that the centrifugal stamen development of the Dilleniales is the only essential character by which the Dilleniales differed from the Ranales.

Since the Dilleniaceae possess a combination of characters particularly

interesting to those concerned with the discipline of comparative morphology and phylogeny (see, e.g., C. Wilson, 1965), it appeared highly advisable to undertake a comprehensive comparative morphological and anatomical study of the family; not only to help clarify those characters already known to exist within the family, but also to attempt to uncover additional evidence which might help elucidate the phylogenetic relationships of the taxa in question. This initial paper concerns the features of phylogenetic value in the woods of the Dilleniaceae.

There are numerous descriptive works dealing with the wood anatomy of the Dilleniaceae, the most notable of which are: Moll and Janssonius (1906); Pearson and Brown (1932); Record and Hess (1943); Metcalfe and Chalk (1950); and Chowdhury and Ghosh (1958). Nevertheless, the wood of this family has neither been adequately described nor fully exploited in attempts to interpret phylogenetic relationships.

Vestal (1937) studied twenty-nine species representing seven genera of Dilleniaceae in reaching his conclusion, based entirely on wood anatomy, that the Guttiferales have a natural alliance with such families as Ochnaceae, Eucryphiaceae, Theaceae, Actinidiaceae, and Saurauaceae, being derived through the dillenis. Bausch (1938), on the other hand, found no similarity in the wood of the Dilleniaceae and that of the Eucryphiaceae. The only other reference to the secondary xylem of this family from a phylogenetic viewpoint is that of Wilson (1960) who found some agreement with the Canellaceae.

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MATERIALS AND METHODS

A total of seventy-one wood samples representing forty species in all ten genera of Dilleniaceae was examined. The writer is extremely thankful to Dr. William L. Stern for his generous personal gift of dilleniaceous wood slides. This collection included samples from the great majority of wood specimens of Dilleniaceae housed in the Samuel James Record Memorial Collection at Yale University. Special thanks are also given to Dr. P. S. Ashton, Kuching, Sarawak, for his contribution of wood from the monotypic *Didesmandra aspera* Stapf, without which this study would have been incomplete. Additional wood samples were obtained from the following sources: the Arnold Arboretum of Harvard University (Aw); Chicago Natural History Museum (Fw); Imperial Forestry Institute, Oxford University (FHow); Division of Forest Products, Commonwealth Scientific and Industrial Research Organization, Melbourne (FPAw); Forest Research Institute, Kepong, Malaya (KEPw); personal collection of Dr. C. L. Wilson (WILSON); Division of Plant Anatomy, Department of Botany, Smithsonian Institution, Washington, D.C. (USw); Yale University, School of Forestry (Yw).

Woods of all ten genera considered by Hoogland (1951) to belong to

the family were examined. However, the semi-herbaceous genera *Acrotrema* and *Pachynema* were represented only by twig material, and were, therefore, used simply for comparative purposes and not studied statistically. As suggested by Stern and Chambers (1960), a complete list of the woods studied, together with pertinent collecting information, is given in APPENDIX 1.

Transverse, radial, and tangential wood sections were cut on a sliding microtome at a thickness ranging from 15 to 30 μ . The sections were stained by first being placed in a mordant of 2 per cent ferric ammonium sulphate (iron alum), after which they were transferred to 0.5 per cent aqueous Heidenhain's haematoxylin and then to a 1 per cent solution of safranin in 50 per cent alcohol. Slides of macerated wood were prepared by putting small slivers into vials containing Jeffrey's macerating fluid (equal parts 10 per cent aqueous nitric and chromic acids) and placing them in an oven at 60°C. The individual xylem elements resulting were washed and stained with a 1 per cent solution of light green in 75 parts clove oil and 25 parts absolute alcohol.

Wood features of phylogenetic value were selected from the compilations of Tipppo (1941, 1946). Measurements of cell length were obtained exclusively from macerated material. All statistical data were derived by measuring twenty-five cells at random from each sample. Tipppo (1941) and Rendle and Clark (1934) recommend that one hundred measurements be taken from each sample in order to get a truly accurate mean length. Because of the small number of wood samples available for study of *Tetracera*, *Schumacheria*, *Didesmandra*, and *Davilla*, the data given for these genera is indicative only of general size ranges. The statistical information on the remaining genera, however, should be considered as truly representative.

Rays are described in accordance with the system of Kribs (1935), as well as by giving a brief written description as advised by the Committee on Nomenclature of the International Association of Wood Anatomists in the *International Glossary of Terms used in Wood Anatomy* (1957). This classification was employed because of its ease of application and wide usage in the literature.

The descriptive terms for the wood parenchyma are those suggested by Hess (1950). In discussing relative cell size, the suggestions of Chattaway (1932), Chalk (1938), and the Committee on the Standardization of Terms of Cell Size (1937) are used. Those adopted in this investigation are given below:

PORE NUMBER

Numerous	more than 40 per mm ²
Many	20-40 per mm ²
Rather many	10-20 per mm ²
Rather few	5-10 per mm ²
Few	2-5 per mm ²
Very few	fewer than 2 per mm ²

VESSEL DIAMETER

Extremely small	up to 25 μ
Very small	25–50 μ
Moderately small	50–100 μ
Medium	100–200 μ
Moderately large	200–300 μ
Very large	300–400 μ
Extremely large	over 400 μ

VESSEL MEMBER LENGTH

Extremely short	less than 175 μ
Very short	175–250 μ
Moderately short	250–350 μ
Medium	350–800 μ
Moderately long	800–1100 μ
Very long	1100–1900 μ
Extremely long	over 1900 μ

LENGTH OF IMPERFORATE TRACHEARY ELEMENTS

Very short	up to 1000 μ
Short	1000–1500 μ
Long	1500–2000 μ
Very long	over 2000 μ

The remainder of the terminology is generally that advocated by the Committee on Nomenclature of the International Association of Wood Anatomists in the *Multilingual Glossary of Terms used in Wood Anatomy* (1964).

OBSERVATIONS

Description of the Wood of Dillenia. Growth rings absent. Wood diffuse-porous; *vessels* (FIGS. 5, 7, 23, 24) solitary, or occasionally in pairs or small clusters, rarely as many as 4 in radial rows, very few to many (1–21, mostly 7–13 per mm²), circular to angular in outline, very small to very large, usually medium-sized (diam. 45–330 μ , mostly 113–228 μ , mean 147 μ); vessel member length medium to extremely long, usually very long (625–3062 μ , mostly 687–2500 μ , mean 1476 μ); tyloses infrequently present. Intervascular pitting (FIG. 8) opposite to transitional, pits circular to elongate (diam. 7–35 μ); pitting to rays similar to scalariform. Perforation plates exclusively scalariform with some branched bars, occasionally nearly reticulate; completely bordered, with 5–120 (mostly 15–40) bars. End wall inclination (FIG. 6) 25–72°. *Imperforate tracheary elements* (FIG. 7) of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits and included or extended, slit-like, often crossed apertures; very short to very long, usually very long (625–4375 μ , mostly 1875–3750 μ , mean 2520 μ). *Rays* (FIG. 6) heterogeneous, Type I, of two sizes; uniseriate rays 1–25 (mostly 4–12) cells high; multiseriate rays 1–18 (mostly 1–10) cells wide, 23 to more than 200 (mostly 52–183) cells high. Multiseriate rays often with long

uniseriate wings composed of upright cells. Elongated upright cells in long series (2–19 cells) often running through multiseriate rays. Crystals in the form of raphides often numerous in ray parenchyma, as are enlarged secretory cells. Ray parenchyma sometimes containing dark, amorphous, gummy deposits. *Wood parenchyma* (FIG. 5) apotracheal diffuse and aggregate diffuse, often paratracheal diffuse to incomplete vasicentric.

The very close similarity of the wood anatomy in the two genera supports Hoogland (1952) in reducing *Wormia* Rottb. to *Dillenia* L.

Description of the Wood of Schumacheria. Growth rings absent. Wood diffuse-porous; *vessels* (FIGS. 1, 22) solitary, apparent pairs due to overlapping ends, rather many to numerous (16–51, mostly 21–41 per mm²); circular in outline, tending to angular, very small to medium, usually moderately small (diam. 30–140 μ , mostly 70–120 μ , mean 90 μ); vessel member length moderately long to very long to extremely long, usually extremely long (1044–3074 μ , mostly 1740–2610 μ , mean 2047 μ). Intervascular pitting scalariform to opposite to transitional, pits circular to elongate (diam. 7–35 μ); pitting to rays opposite to transitional to scalariform. Perforation plates exclusively scalariform, bars commonly branched, completely bordered, with 34–135 (avg. 40–60) bars. End wall inclination 35–75°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits and extended, slit-like, often crossed pit apertures; long to very long, usually very long (1160–3480 μ , mostly 2030–2900 μ , mean 2380 μ). *Rays* (FIG. 2) heterogeneous, Type I, of two sizes; uniseriate rays 5–28 (mostly 10–15) cells high; multiseriate rays 1–5 cells wide, 35–68 (mostly 50–60) cells high; multiseriate rays often with extremely long uniseriate wings composed of upright cells. *Wood parenchyma* apotracheal diffuse.

Description of the Wood of Hibbertia. Growth rings present or absent, when present not well defined. Wood diffuse-porous; *vessels* (FIG. 3) mostly solitary, with some apparent pairs due to overlapping ends, very small clusters infrequently present, rather few to numerous (5–40, mostly 10–20 per mm²); circular to angular in outline, very small to medium sized (diam. 30–165 μ , mostly 60–135 μ); vessel member length medium to very long, usually moderately long (625–1562 μ , mostly 812–1437 μ , mean 1074 μ). Intervascular pitting opposite to transitional to scalariform, pits circular to scalariform (diam. 8–40 μ), pitting to rays similar. Perforation plates exclusively scalariform, completely bordered to only bordered at the ends, with 15–88 (mostly 35–50) bars. Bars commonly branched to nearly reticulate. End wall inclination 45–85°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits with extended or included, slit-like, often crossed, pit apertures; very short to very long, usually long (625–2150 μ , mostly 1250–1875 μ , mean 1551 μ). *Rays* (FIG.

4) heterogeneous, Type I, of two sizes; uniseriate rays 1–8 (mostly 2–7) cells high; multiseriate rays 1–5 (mostly 1–3) cells wide, 7–34 (mostly 15–30) cells high. Multiseriate rays often with long uniseriate wings. Ray parenchyma frequently contains dark, amorphous, gummy deposits. *Wood parenchyma* apotracheal diffuse; crystals in the form of raphides sometimes present in enlarged wood parenchyma cells.

Description of the Wood of Didesmandra. Growth rings absent. Wood diffuse-porous; *vessels* solitary, rarely in pairs, apparent pairs due to vessel overlap, rather many to numerous (13–65, mostly 25–45 per mm²); angular in outline, very small to moderately small, usually moderately small (diam. 30–90 μ , mostly 45–70 μ , mean 60 μ); vessel member length medium to extremely long, usually very long (780–2600 μ , mostly 1150–2250 μ , mean 1574 μ). Intervascular pitting scalariform to opposite; pitting to rays similar. Perforation plates exclusively scalariform. Bars commonly anastomosing to reticulate; completely bordered, with 25–160 (mostly 57–120) bars. End wall inclination 30–75°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, mostly thin-walled; fiber tracheids with distinctly bordered pits and included or extended, slit-like, often crossed, pit apertures; short to very long, mostly very long (1400–3050 μ , mostly 1800–2870 μ , mean 2292 μ). *Rays* heterogeneous, Type I, of two sizes; uniseriate rays 2–33 (mostly 6–21) cells high; multiseriate rays 1–15 (mostly 3–10) cells wide, 14–83 cells high. Main body of multiseriate rays composed of both procumbent and upright cells, often with long uniseriate wings composed of upright cells. Crystals in the form of raphides infrequently present in ray tissue. Ray parenchyma sometimes containing dark, amorphous, gummy deposits. *Wood parenchyma* apotracheal diffuse.

Description of the Secondary Xylem of Acrotrema and Pachynema. Growth rings absent. Wood diffuse-porous; *vessels* (Figs. 9–12) solitary to rarely in pairs, apparent pairs due to vessel overlap; circular to angular in outline, extremely small to very small (diam. 11–34 μ , mostly 20–27 μ). Intervascular pitting (Fig. 13) scalariform to opposite to rarely transitional, pits circular to elongate (diam. 7–18 μ). Perforation plates exclusively scalariform, with 16–48, completely bordered, bars. Bars sometimes anastomosing. *Imperforate tracheary elements* of the fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits with included, or extended, slit-like, often crossed, apertures. In *Acrotrema*, elements were found with greatly extended pit apertures and much reduced pit borders. *Rays* reduced to mostly uniseriate with occasional biseriate rays. Rays composed of both procumbent and upright cells, 1–14 cells high. *Wood parenchyma* apotracheal diffuse. Crystals in the form of raphides observable in the periderm of *Acrotrema*.

Description of the Wood of Doliocarpus. Growth rings absent. Two samples (*D. coriaceus* (Mart. & Zucc.) Gilg and *D. sp.*, Yw 39903)

exhibit successive cambial activity which resulted in concentric zones of included phloem, conjunctive tissue, and sclerotic cells. Wood diffuse-porous; *vessels* (FIG. 26) solitary, very few to rather many (2–20, mostly 4–9 per mm²); circular in outline, moderately small to extremely large, usually moderately large (diam. 50–555 μ , mostly 150–450 μ , mean 256 μ); vessel member length medium to very long, usually moderately long (362–1812 μ , mostly 687–1250 μ , mean 917 μ). Intervascular pitting (FIG. 21) opposite to transitional, pits circular to elongate (diam. 7–40 μ); pitting to rays similar. Perforation plates mostly simple, scalariform in the smaller vessels. Scalariform plates with 1–15 bars, sometimes branched, completely bordered to bordered only at the ends. End wall inclination 35–90°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits and extended, slit-like, often crossed, pit apertures, very short to very long, usually short (687–4000 μ , mostly 1125–1562 μ , mean 1471 μ). *Rays* heterogenous, Type I and IIA, of two sizes; uniseriate rays 1–9 (mostly 3–7) cells high; multiseriate rays 1–41 (mostly 1–35) cells wide, 36 to over 500 (mostly 45–200) cells high. Crystals in the form of raphides often very numerous, as are enlarged secretory cells. *Wood parenchyma* mostly apotracheal diffuse, some paratracheal diffuse.

One sample studied, identified with an unpublished name (Yw 39903), displayed features inconsistent with those of the other species examined. The radial pore chains and pore clusters, vasicentric parenchyma, and significantly different vessel member and fiber length suggest that it is not a member of this genus. The accompanying data stated it was taken from Fw 11189. However, the two wood samples were clearly not taken from the same specimen.

Description of the Wood of Davilla. Growth rings absent. Wood diffuse-porous; *vessels* (FIGS. 15, 23) solitary, rather few to rather many (3–16, mostly 4–8 per mm²); circular in outline, very small to extremely large, usually moderately large (diam. 30–450 μ , mostly 222–382 μ , mean 284 μ); vessel member length medium to moderately long, usually medium-sized (437–1062 μ , mostly 625–937 μ , mean 777 μ). Intervascular pitting opposite to transitional, pits circular to elongate (10–25 μ); pitting to rays similar. Perforation plates mostly simple, scalariform in the smaller vessels. Scalariform perforation plates with 5–10 bars, completely bordered to bordered only at the ends. End wall inclination 55–90°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin-walled; fiber tracheids with distinctly bordered pits with extended or included, slit-like, often crossed, pit apertures; very short to very long, usually long (938–2625 μ , mostly 1250–2375 μ , mean 1613 μ). *Rays* (FIG. 15) heterogeneous, Type I and IIA, of two sizes; uniseriate rays 1–31 (mostly 15–30) cells high; multiseriate rays 1–38 (mostly 1–31) cells wide, 75 to over 500 (mostly 200–450) cells high. Large sclerotic cells infrequently present in ray tissue, quite common in bark. Ray cells often containing large

secretory cells and dark, amorphous, gummy deposits. *Wood parenchyma* apotracheal diffuse to scattered paratracheal diffuse.

Description of the Wood of *Curatella*. Growth rings absent. Wood diffuse-porous; *vessels* (FIG. 14) solitary, or rarely in clusters of up to three vessels, very few to rather many (1–15, mostly 2–7 per mm²), circular to rarely angular in outline, very small to very large, usually medium-sized (diam. 45–360 μ , mostly 145–200 μ , mean 180 μ); vessel member length very short to very long, usually medium-sized (250–1312 μ , mostly 625–900 μ , mean 725 μ). Intervascular pitting opposite to transitional, pits circular to elongate (diam. 8–25 μ); pitting to rays similar. Perforation plates mostly simple (FIG. 17), scalariform in the smaller vessels. Scalariform perforation plates completely bordered, with 1–12 (mostly 1–5) bars, branching of bars common, occasionally reticulate perforations are present. Inclination of end walls 55–90°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits with extended, slit-like, often crossed, pit apertures; very short to very long, usually long (562–2750 μ , mostly 1354–2208 μ , mean 1805 μ). Rays (FIG. 16) heterogeneous, Type I and IIA, of two sizes; uniseriate rays 1–20 (mostly 1–11) cells high; multiseriate rays 1–20 (mostly 1–15) cells wide, 32–279 (mostly 54–119) cells high. Crystals in the form of raphides often numerous, as are enlarged secretory cells. Ray parenchyma often containing dark, amorphous, gummy deposits. *Wood parenchyma* (FIG. 14) aggregate to narrow-banded apotracheal, some paratracheal diffuse.

Description of the Wood of *Tetracera*. Growth rings absent or present; if present, not well defined. One species (*T. volubilis* L.) exhibited successive cambial activity which resulted in concentric zones of included phloem, conjunctive parenchyma with scattered fibers, and sclerotic cells. Wood diffuse-porous; very weak ring-porosity in one species (*T. boiviniana* Baill.) as shown by larger vessel diameter in the spring wood. *Vessels* (FIGS. 18, 27) solitary, rarely in pairs, few to rather many (3–11, mostly 5–8 per mm²); circular in outline, very small to very large (diam. 50–350 μ); vessel member length very short to moderately long, usually medium-sized (220–1062 μ , mostly 370–937 μ , mean 565 μ). Intervascular pitting opposite to transitional, pits circular to elongate (diam. 7–35 μ); pitting to rays similar. Perforation plates mostly simple, scalariform in the smaller vessels. Scalariform plates completely bordered, with 1–20 (mostly 1–10) bars. Vessel members occasionally with reticulate or “multiperforate” perforation plates (FIG. 19). Inclination of end walls 35–90°. *Imperforate tracheary elements* of the tracheid, vasicentric tracheid, and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits and extended or included, slit-like, often crossed, pit apertures; very short to long, usually short (500–1625 μ , mostly 625–1250 μ , mean 1003 μ). Rays (FIG. 20) heterogeneous, Type I and IIA, of two sizes; uniseriate rays 1–18 (mostly 3–11) cells high;

multiseriate rays 1–13 (mostly 1–10) cells wide, 20–152 (mostly 45–110) cells high. Multiseriate rays often containing large secretory cells. Crystals in the form of raphides numerous along with dark, amorphous, gummy deposits. Series of upright cells sometimes running through rays. *Wood parenchyma* apotracheal diffuse.

The small number of wood samples studied in this genus revealed a relatively large variability in anatomical structure. The extent and significance of this variation can only be determined by the examination of additional samples and species when they become available.

DISCUSSION

The woods of the Dilleniaceae reveal a rather low level of specialization. This is supported by the occurrence in all woods of the following primitive features: (1) wood diffuse-porous; (2) predominantly solitary pores; (3) opposite-transitional intervascular pitting; (4) fiber tracheids; (5) heterogeneous Type I or IIA rays; and (6) wood parenchyma mostly apotracheal diffuse. Despite this apparent homogeneity, it is quite obvious that considerable variation exists between genera in vessel member structure.

Since the trends of vessel specialization were initially discovered for dicotyledons by Bailey and Thompson (1918), Bailey and Tupper (1918), and Frost (1930, 1931), and for monocotyledons by Cheadle (1942, 1943a, 1943b, 1944), the vessel has been an invaluable tool for interpreting phylogenetic relationships. The importance ascribed to the vessel member in this regard results not only from a thorough understanding of vessel phylogeny, but more importantly from the fact that these clearly defined trends are both unidirectional and irreversible.

It is of great interest, therefore, to find vessels within a single family which reveal salient irreversible trends of specialization. On the basis of vessel member structure, as well as more subtle wood characters, the Dilleniaceae are most conveniently segregated into the two subfamilies as suggested by Hoogland (1952, 1953). The anatomical features of the two subfamilies are summarized in TABLE 2.

I. COMPARISON OF THE TWO SUBFAMILIES OF DILLENIACEAE

The most primitive forms of vessel members are found in the subfamily Dillenioideae. In this group the vessels are angular to circular in outline, of very great length (mean 1532μ), possess exclusively scalariform perforation plates, with up to 160 bars, are mostly completely bordered, have very oblique end walls, and have scalariform to opposite to transitional intervascular pitting. The extremely tracheid-like vessel members of *Schumacheria* and *Didesmandra* are the least specialized in the family. The vessel members in the genera *Dillenia* and *Hibbertia* are, in general, only slightly more advanced.

The Tetraceroideae are characterized by certain salient trends of vessel

TABLE 2. — Comparison of Averages of Characters of Wood Anatomy of the Two Subfamilies of Dilleniaceae

CHARACTER	DILLENIOIDEAE	TETRACEROIDEAE
VESSEL MEMBERS		
1. Distribution	mostly solitary	mostly solitary
2. Shape in outline	circular to angular	circular
3. Type of perforation plate	scalariform only	scalariform and simple
4. Bars in perforation plate		
Lowest average	18	2
Mean averages	40	5
Highest average	123	9
5. End wall inclination . . .	30–80°	50–90°
6. Length		
Range	625–3074 μ	220–1812 μ
Most frequent range . . .	687–2610 μ	370–1250 μ
Mean	1532 μ	766 μ
7. Width		
Range	30–330 μ	30–555 μ
Most frequent range . . .	60–228 μ	145–450 μ
Mean	124 μ	240 μ
8. Intervascular pitting . .	scalariform-transitional	opposite-transitional
WOOD FIBERS		
9. Type	fiber tracheid	fiber tracheid
10. Wall thickness	thin to thick	mostly thin
11. Length		
Range	625–4375 μ	500–4000 μ
Most frequent range . . .	1250–3750 μ	625–2375 μ
Mean	2150 μ	1473 μ
WOOD RAY		
12. Type	Type I	Type I and IIA
13. Average width of multi- seriate rays (no. of cells)	1–18 (avg. 9)	1–41 (avg. 22)
14. Average height of multi- seriate rays (no. of cells)	7–200 (avg. 39–91)	20–500 (avg. 86–219)
WOOD PARENCHYMA		
15. Distribution	mostly apotracheal diffuse	mostly apotracheal diffuse

member specialization. The four genera included in this subfamily all possess vessel members with both simple and scalariform perforations. In all, simple perforations are considerably more numerous than the scalariform type, which are confined strictly to the smaller vessels of the secondary xylem. When scalariform plates do occur, they seldom have more than ten bars. A small number of vessel members were observed which bore scalariform and simple perforation plates at opposite ends. All gradations

from porous-oblique to transverse-porous perforation plates are present. Correlated with the change in type of perforation plate is a significant decrease in length (mean 766μ) with a considerable increase in width. The transectional outline is predominantly circular. Whereas *Doliocarpus*, *Davilla*, and *Curatella* are intermediate in the above features, the genus *Tetracera* appears to be the most advanced of all Dilleniaceae in vessel structure. The last-named genus is also unique in its possession of so called "multiperforate" or reticulate perforations. The significance of this type of perforation plates is still a matter of controversy. Thompson (1923) suggested that they may represent modifications of scalariform types or retrogressions from simple plates. Gottwald and Parameswaran (1964), in describing their occurrence in the Dipterocarpaceae, believe they are intermediate forms between scalariform and simple perforations.

That all known trends of vessel specialization do not always occur simultaneously (Bailey and Howard, 1941; Bailey, 1944) is well exemplified by the existence of opposite-transitional, lateral-wall pitting in both subfamilies.

Bailey (1957) pointed out that in certain specialized cases, such as lianas, vessel members may become quite transformed as a result of their habit, and do not, therefore, indicate true phylogenetic advancement. Ayensu and Stern (1964) encountered such modification in their study of the scandent Passifloraceae, and so considered the presence of shorter, broader, solitary vessel members in this group to be related to the physiology of their habit rather than to their phylogenetic position. They indicate, however, that habit-related anatomical modification may be superimposed upon phylogenetic specialization and the separation of these facets is often difficult.

Since the Dilleniaceae range from large trees to scandent lianas, with all intermediate forms, it is quite possible that the advancement exhibited by certain species of *Davilla*, *Doliocarpus*, and *Tetracera* is actually coordinated with habit. However, the occurrence of scalariform perforation plates in these genera would also seem to indicate that they are really in an intermediate stage of advancement. Furthermore, similar advanced vessel types were observed in *Curatella*, which may be a small tree up to eight meters in height (Standley, 1928).

It is clear, therefore, that it would be erroneous to attempt to interpret phylogenetic position of the woods from vessel structure alone. It is necessary to correlate this evidence with that obtained from other features of the xylem.

The unspecialized nature of the Dilleniaceae is indicated by the presence of the longest imperforate tracheary elements and by the exclusively heterogeneous Type I rays (except in the reduced *Acrotrema* and *Pachynema*). Both uniseriate and multiseriate rays are of extreme height. In addition, the multiseriate rays are often conspicuous by their long uniseriate wings composed of upright cells. Although the tremendously high and broad rays of the Tetraceroideae are the largest in the family, there is a marked tendency for reduction in the uniseriate wings and an increased

uniformity in the ray cells to a point where more advanced Type IIA rays are present.

Both subfamilies have predominantly apotracheal diffuse parenchyma. Within the Dilleniaceae, only *Dillenia* is characterized by paratracheal diffuse parenchyma, whereas in the Tetraceraceae both *Davilla* and *Doliocarpus* show this condition. Also, *Curatella* exhibits fairly specialized aggregate to narrow-banded apotracheal with some paratracheal diffuse parenchyma.

Crystals in the form of raphides are often quite numerous in the wood of the Dilleniaceae. Although Chattaway (1955) states that crystals have been reported in approximately 1000 genera of 160 families, the presence of certain types of crystals, such as raphides, is much less common and may, therefore, be of more taxonomic value (Metcalf and Chalk, 1950; Chattaway, 1955). Raphides are undoubtedly diagnostic for the majority of genera within the family, but are of questionable taxonomic importance for the family as a whole. The only two genera in which raphides were not confirmed are *Davilla*, where they have been reported (cited by Chattaway, *loc. cit.*) and *Schumacheria*. In addition, any one genus may not possess raphides uniformly in all species (e.g., *Dillenia*). When present, these needle-shaped crystals are more commonly found in large, mucilage-containing ray cells. Enlarged, raphide-bearing wood parenchyma strands were observed only in certain species of *Hibbertia*. However, the occurrence of crystals in such a large number of unrelated plant families seems to negate any phylogenetic significance in this anatomical character.

Secretory cells were similarly encountered in all dilleniaceous genera except *Schumacheria* and *Didesmandra*. Stern (1954a) advised the term "secretory intercellular cavity" be used when the chemical composition of the secretion is not known. The darkly staining amorphous mucilage may be deposited either in ray parenchyma, axile parenchyma, or vessels (Fig. 18). The presence of this mucilage is apparently not uniform within genera or even in species. Canright (1955) considered oil cells to be of no phylogenetic significance in the wood of the Magnoliaceae. Stern (1954b), however, suggested they may represent a particular kind of specialization in lauraceous wood. The occurrence of secretory cells in the Dilleniaceae offers little evidence to support either concept. However, it is of importance to mention that secretory cells are common features of all organs of most families generally regarded as ranalian; on the other hand, this feature is relatively rare in families in the higher orders, e.g., Guttiferae.

II. COMPARISON OF WOOD OF THE DILLENiaceae WITH THAT OF PUTATIVELY RELATED FAMILIES

The following discussion will attempt to evaluate, on the basis of wood anatomy, the relationships of the Dilleniaceae to many putatively related families. In the majority of cases, woods of the various families were actually examined. In addition to these personal observations, descrip-

tions were obtained from the following sources: Canright (1955), Chatterway (1937), Keng (1962), Metcalfe and Chalk (1950), Swamy and Bailey (1949), Vander Wyk and Canright (1956), and Vestal (1937).

The Dilleniaceae have been placed, at one time or another, mainly on the basis of gross floral morphology, with the following ranalian families: Ranunculaceae, Magnoliaceae, Winteraceae, Calycanthaceae, Annonaceae, Canellaceae, Cercidiphyllaceae, and Ceratophyllaceae. Evidence from wood anatomy, for the most part, does not support such alliances.

The vesselless Winteraceae and aquatic Ceratophyllaceae may be readily dismissed as showing little similarity to the Dilleniaceae.

The presence of simple perforation plates, alternate intervacular pitting, libriform wood fibers and paratracheal parenchyma in the Ranunculaceae (excluding *Paeonia*) indicates that the xylem of this family is on a higher level of advancement than that of the Dilleniaceae.

The Calycanthaceae do possess fiber tracheids, heterogeneous Type I rays, and apotracheal diffuse to vasicentric scanty parenchyma, but, on the other hand, show pores mostly in radial multiples with exclusively simple perforation plates, alternate intervacular pitting, as well as uniformly occurring vasicentric tracheids.

The Magnoliaceae are characterized by wood which shows transitions from comparatively primitive to rather advanced. Although the most primitive genera do have some similarities with the Dilleniaceae, the family appears to be well placed near the Degeneriaceae and Himantandraceae (Bailey, Nast and Smith, 1943; Canright, 1955).

The Annonaceae, likewise, is anatomically advanced over the Dilleniaceae and accordingly, was considered by Vander Wyk and Canright (1956) to share more common features with the Myristicaceae.

Although Wilson (1960) did find several points of agreement between the Dilleniaceae and Canellaceae, he found the wood features in the latter family had the greatest degree of similarity with the Illiciaceae and Eupteleaceae.

The wood of the Cercidiphyllaceae approaches the Dilleniaceae in primitive vessel structure and the presence of fiber tracheids, but differs in the terminal wood parenchyma and heterogeneous Type IIB rays (Swamy and Bailey, 1949).

Due to the large degree of family overlap in ordinal concepts, it will be more meaningful for the remaining discussion to consider relationships of individual families irrespective of specific orders.

There is little similarity between the wood of the Sterculiaceae and that of the Dilleniaceae. Such features as exclusively simple perforation plates, alternate intervacular pitting, abundant parenchyma in uniseriate lines and in some cases together with distinct vasicentric sheaths, Type IIA or IIB rays, and libriform wood fibers, are much more advanced than those of the Dilleniaceae.

The Ochnaceae and Connaraceae are also anatomically on a higher level of advancement than the Dilleniaceae as evidenced by the occurrence in both families of the following features: typically simple perforation plates,

alternate intervascular pitting, and libriform wood fibers (exclusively in the Connaraceae and partially in the Ochnaceae. The Connaraceae is further characterized by highly advanced heterogeneous Type III or homogeneous Type III rays.

Although the Eucryphiaceae and Brunelliaceae are not as advanced anatomically as the previous families, they are still more highly developed than the Dilleniaceae. Woods of both families contain both simple and scalariform perforation plates. The parenchyma of the Eucryphiaceae is diffuse or slightly banded to terminally banded, whereas wood parenchyma is absent from the Brunelliaceae. Both families have genera with occasional heterogeneous Type III rays. However, other lines of evidence, viz., floral morphology and chemical data, support placing these two families near the Cunoniaceae (Bausch, 1938).

The genera *Saurauia* and *Actinidia* have often been placed near, if not included in, the Dilleniaceae. Such wood features in *Saurauia* as mostly solitary pores, vessel members of extreme length and exclusively scalariform perforation plates (with up to 90 bars), scalariform to opposite to transitional intervascular pitting, long fiber tracheids, exclusively heterogeneous Type I rays, and apotracheal diffuse parenchyma, are very primitive; comparable features are found only in the most unspecialized members of the Dilleniaceae.

Actinidia shows features more in common with the Tetraceroideae, such as solitary pores, both simple and scalariform perforation plates, fiber tracheids of similar mean length, and heterogeneous Type I or IIA rays. At the same time, however, *Actinidia* also has some wood characters not shared with any genera in the afore-mentioned subfamily. These include scalariform perforation plates which may have over 75 bars, and much reduced ray structure.

In contrast to the above, the alliance of the Dilleniaceae to the Theaceae is supported by anatomical considerations. Keng (1962) compared the wood of members of this family and found the wood of the Camelliaceae to be, in general, more advanced than that of the Ternstroemiaceae. Furthermore, although the wood of the Theaceae is considered to be relatively primitive, there are specific cases of high advancement. The greatest agreement between the Dilleniaceae and Theaceae exists between the Dilleniaceae and tribes Adinandrieae and Ternstroemiaceae. This similarity is evident in the mostly solitary pores, exclusively scalariform perforation plates with many bars, similar mean vessel member length (Adinandrieae), scalariform to opposite intervascular pitting, uniform occurrence of fiber tracheids of similar mean length, heterogeneous Type I rays (significantly broader and higher in the Dilleniaceae), and wood parenchyma mostly apotracheal diffuse.

The occurrence of spiral thickenings in the vessels of some Theaceae is a character of questionable phylogenetic significance (Canright, 1955; Keng, 1962; Stern, 1954b). This character was not encountered in any of the Dilleniaceae observed but does show up in the vessels of *Saurauia* and *Actinidia*.

Recent systems have repeatedly linked the monotypic family Crossosmataceae to the Dilleniaceae by the presence in the genus *Crossosoma* of free follicular carpels and strongly arillate seeds. However, the semi-ring porosity, exclusively simple perforation plates, mostly alternate intervascular pitting, very short imperforate tracheary elements, heterogeneous Type IIB rays, very sparse to absent parenchyma are features clearly more advanced than those of the Dilleniaceae. If *Crossosoma* were closely related to the Dilleniaceae, it would seem that its secondary xylem should retain more of the primitive features found in that family.

Since being removed from the Ranunculaceae, the genus *Paeonia* is now most commonly placed as a monotypic family in close association with the Dilleniaceae. Examination of the wood reveals that it is more highly evolved than the Dilleniaceae in a number of characters: reduced ray structure (uniseriate or biseriate rays commonly occur), occasional alternate intervascular pitting, reduction in the number of scalariform bars in the perforation plates to 1 to 5, vessels occasionally in small clusters with semi-ring porosity. In spite of these features, wood anatomy does not negate the possible position of *Paeonia* as allied to, yet more highly advanced than, the Dilleniaceae.

Since a taxon which retains primitive wood characters cannot be derived from one which is uniformly advanced, Bailey (1957) has pointed out that the evidence obtained from wood studies are often more helpful in negations than in positive assertions of close alliance. Furthermore, structures often appear similar in quite distantly related groups owing to the frequent occurrence of parallel evolution (Bailey, *loc. cit.*). It would, therefore, be very unwise to speculate concerning phyletic relationships solely on the basis of wood anatomy. Bailey (1951, 1953, 1957) and Canright (1955, 1963) have stressed the need for comprehensive studies which take into account evidence from all organs and parts of the plant. Only when all the information has been gathered and carefully evaluated can meaningful phylogenies be constructed.

APPENDIX 1. — Dilleniaceous Wood Examined

SPECIES	COLLECTOR AND NUMBER	GEOGRAPHICAL ORIGIN	HERBARIUM VOUCHER	LOCATION AND CATALOG NUMBER
<i>Acrotrema uniflorum</i> Hook.	Thwaites 265	Ceylon	—	Aw 26224
<i>Curatella americana</i> L.	A. C. Smith 2185	British Guiana	Y	Yw 35484
<i>C. americana</i> L.	Zanderij 209	Surinam	Y	Yw 41257
<i>C. americana</i> L.	L. Williams 9842	Mexico	Y	Yw 35006
<i>C. americana</i> L.	A. J. Fors 96	Cuba	—	USw 21446
<i>C. americana</i> L.	H. Pittier	Venezuela	Y	USw 2773
<i>C. americana</i> L.	Forest Dept. 2185	British Guiana	—	FHOW 14636
<i>C. americana</i> L.	B. A. Krukoff	—	—	Fw 2055
<i>Davilla aspera</i> (Aubl.) Benoist	Cuatrecasas 17302	Colombia	F, VALLE	Yw 43186
<i>D. aspera</i> (Aubl.) Benoist	Cuatrecasas 17302	Colombia	F, VALLE	Fw 17302
<i>D. aspera</i> (Aubl.) Benoist	Woytkowski 5461	Peru	MO	USw 15527
<i>D. rugosa</i> Poir.	H. León	Cuba	—	Yw 40712
<i>Didesmandra aspera</i> Stapf	Banying anak Ludong	Sarawak	—	s. n.
<i>Dillenia aurea</i> Smith	—	Java	—	Yw 30030
<i>D. biflora</i> (A. Gray) Martelli ex Dur. & Jacks.	—	Fiji	—	Yw 25835
<i>D. biflora</i> (A. Gray) Martelli ex Dur. & Jacks.	A. C. Smith 3471	Fiji	NY	Yw 28327
<i>D. biflora</i> (A. Gray) Martelli ex Dur. & Jacks.	—	Fiji	—	Yw 25674
<i>D. excelsa</i> (Jack) Gilg	—	Java	—	Yw 30025
<i>D. excelsa</i> (Jack) Gilg	—	Java	—	Yw 30026
<i>D. excelsa</i> (Jack) Gilg	—	Java	—	Yw 30027
<i>D. excelsa</i> (Jack) Gilg	B. A. Krukoff 271	Sumatra	NY	USw 7127
<i>D. excelsa</i> (Jack) Gilg	B. A. Krukoff 271	Sumatra	NY	FHOW 8368

SPECIES	COLLECTOR AND NUMBER	GEOGRAPHICAL ORIGIN	HERBARIUM VOUCHER	LOCATION AND CATALOG NUMBER
<i>D. excelsa</i> (Jack) Gilg	D. E. Carver 20	Sarawak	—	FHOw 6655
<i>D. eximia</i> Miq.	—	Malaya	—	KEPw 7302
<i>D. indica</i> L.	—	Java	—	Yw 30028
<i>D. indica</i> L.	—	Malaya	—	KEPw 5968
<i>D. ingens</i> (B. L. Burtt) A. C. Smith	Waterhouse 25	Bougainville	Y	Yw 21156
<i>D. ingens</i> (B. L. Burtt) A. C. Smith	F. S. Walker 146	Solomons	—	FHOw 17958
<i>D. luzoniensis</i> (Vidal) Martelli ex Dur. & Jacks.	—	Philippines	—	Fw 272982
<i>D. pentagyna</i> Roxb.	—	Java	—	Yw 30032
<i>D. pentagyna</i> Roxb.	J. F. Kools 33	Indonesia	—	FHOw 18866
<i>D. philippinensis</i> Rolfe	—	Philippines	—	USw 5213
<i>D. pulchella</i> (Jack) Gilg	H. E. Desch. 41887	Malaya	KEP	Yw 38502
<i>D. pulchella</i> (Jack) Gilg	H. E. Desch. 41887	Malaya	KEP	KEPw 3675
<i>D. pulchella</i> (Jack) Gilg	—	Malaya	—	KEPw 6544
<i>D. quercifolia</i> (White & Francis ex Lane-Poole) Hoogl.	Holland	New Britain	—	USw 22228
<i>D. quercifolia</i> (White & Francis ex Lane-Poole) Hoogl.	—	—	—	FPAw 6437
<i>D. reticulata</i> King	Forest Dept. 422	Malaya	FHO	FHOw 7602
<i>D. reticulata</i> King	—	Malaya	—	KEPw 7261
<i>D. reticulata</i> King	—	Malaya	—	KEPw 5779
<i>D. retusa</i> Thunb.	—	Ceylon	—	Yw 9781
<i>D. scabrella</i> (D. Don) Roxb. ex Wall.	Forest Dept. 607	Burma	—	FHOw 1676
<i>D. solomonensis</i> (White) Hoogl.	—	Solomon Is.	—	FPAw 8226
<i>D. solomonensis</i> (White) Hoogl.	F. S. Walker 145	Solomon Is.	—	FHOw 17957
<i>D. sumatrana</i> Miq.	—	—	—	KEPw 403

<i>D. sumatrana</i> Miq.	—	—	—	KEPw 382
<i>D. triquetra</i> (Rottb.) Gilg	—	Ceylon	—	Yw 9807
<i>D. triquetra</i> (Rottb.) Gilg	—	Ceylon	—	USw 21889
<i>D. turbinata</i> Finet & Gagnep.	Sun Yatsen Univ. 0835	Hainan	SYS	Yw 29564
<i>D. turbinata</i> Finet & Gagnep.	Tang	China	Fan Mem. Inst. Chungking	USw 8597
<i>Doliocarpus</i> sp.	S. J. Record	British Honduras	—	Yw 8831
<i>Doliocarpus</i> sp.	A. Ducke 327	Brazil	Y	Yw 34091
<i>Doliocarpus</i> sp.	B. A. Krukoff 7020	Brazil	US	Yw 37027
<i>D. coriaceus</i> (Mart. & Zucc.) Gilg	Cuatrecasas 16556	Colombia	F, VALLE	Yw 43052
<i>D. dentatus</i> (Aubl.) Standl.	Stern et al. 549	Panama	US, MO	USw 16329
<i>D. lasiogyne</i> Benoist	Reitz & Klein 5776	Brazil	HBR	USw 15034
<i>D. major</i> Gmel.	Stern et al. 844	Panama	MO	USw 16485
<i>D. olivaceus</i> Sprague & Wms. ex Standl.	Stern et al. 11	Panama	MO	USw 16042
<i>Doliocarpus</i> sp.	B. A. Krukoff 11189	Bolivia	NY	Fw 11189
<i>Hibbertia coriacea</i> (Hook. f.) Gilg	—	New Caledonia	—	FPAw 23183
<i>H. cuneiformis</i> Sm.	—	Pemberton, W. Australia	—	FPAw 11684
<i>H. lucens</i> Brongn. & Griseb.	A. C. Smith 3546	Fiji	NY	Yw 28402
<i>H. lucens</i> Brongn. & Griseb.	A. C. Smith 3045	Fiji	NY	Yw 27903
<i>H. lucens</i> Brongn. & Griseb.	—	New Caledonia	—	FPAw 12037
<i>H. saligna</i> R. Br. ex DC.	—	New South Wales	—	FPAw 13034
<i>H. tetrandra</i> (Lindl.) Gilg	Wilson 848	—	US	WILSON 848
<i>Pachynema complanatum</i> R. Br. ex DC.	Von Mueller	New South Wales	A	Aw 26225
<i>Schumacheria castaneifolia</i> Vahl	—	Ceylon	—	Aw 2632
<i>Tetracera boiviniana</i> Baill.	H. J. Schlieben 5187	Tanganyika	Y	Yw 29962
<i>T. scandens</i> (L.) Merr.	—	Philippines	—	s. n.
<i>T. volubilis</i> L.	H. León	Cuba	—	Yw 40713

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EXPLANATION OF PLATES

PLATE I

FIGS. 1-4. 1, *Schumacheria castaneifolia* Vahl, cross section of wood showing solitary, angular vessels and sparse apotracheal parenchyma, $\times 130$. 2, the same, tangential section showing narrow heterogeneous rays and highly oblique end wall of vessel member, $\times 130$. 3, *Hibbertia lucens* Brongn. & Griseb., cross section of wood illustrating mostly solitary pores, $\times 130$. 4, the same, radial section, $\times 70$.

PLATE II

FIGS. 5-8. 5, *Dillenia ingens* (B. L. Burtt) A. C. Smith, cross section of wood showing solitary vessels, apotracheal and paratracheal parenchyma, $\times 60$. 6, the same, tangential section showing heterogeneous rays and oblique angle of many-barred scalariform perforation plate, $\times 60$. 7, *Dillenia biflora* (A. Gray) Martelli ex Dur. & Jacks., cross section of wood illustrating solitary pores, thick-walled fiber tracheids, apotracheal parenchyma, and dark-staining deposits in ray parenchyma, $\times 100$. 8, *Dillenia turbinata* Finet & Gagnep., longitudinal section of wood showing sparse opposite to transitional intervacular pitting, $\times 400$.

PLATE III

FIGS. 9-13. 9, *Acrotrema uniflorum* Hook., cross section of stem with limited secondary xylem; note narrow rays, $\times 400$. 10, *Pachynema complanatum* R. Br. ex DC., cross section of stem with limited secondary xylem, $\times 400$. 11, *Acrotrema uniflorum*, longitudinal section of stem illustrating oblique angle of many-barred scalariform perforation plate, $\times 400$. 12, the same, longitudinal section of stem showing scalariform perforation plate, $\times 400$. 13, *Pachynema complanatum*, longitudinal section of stem showing scalariform to opposite intervacular pitting, $\times 400$.

PLATE IV

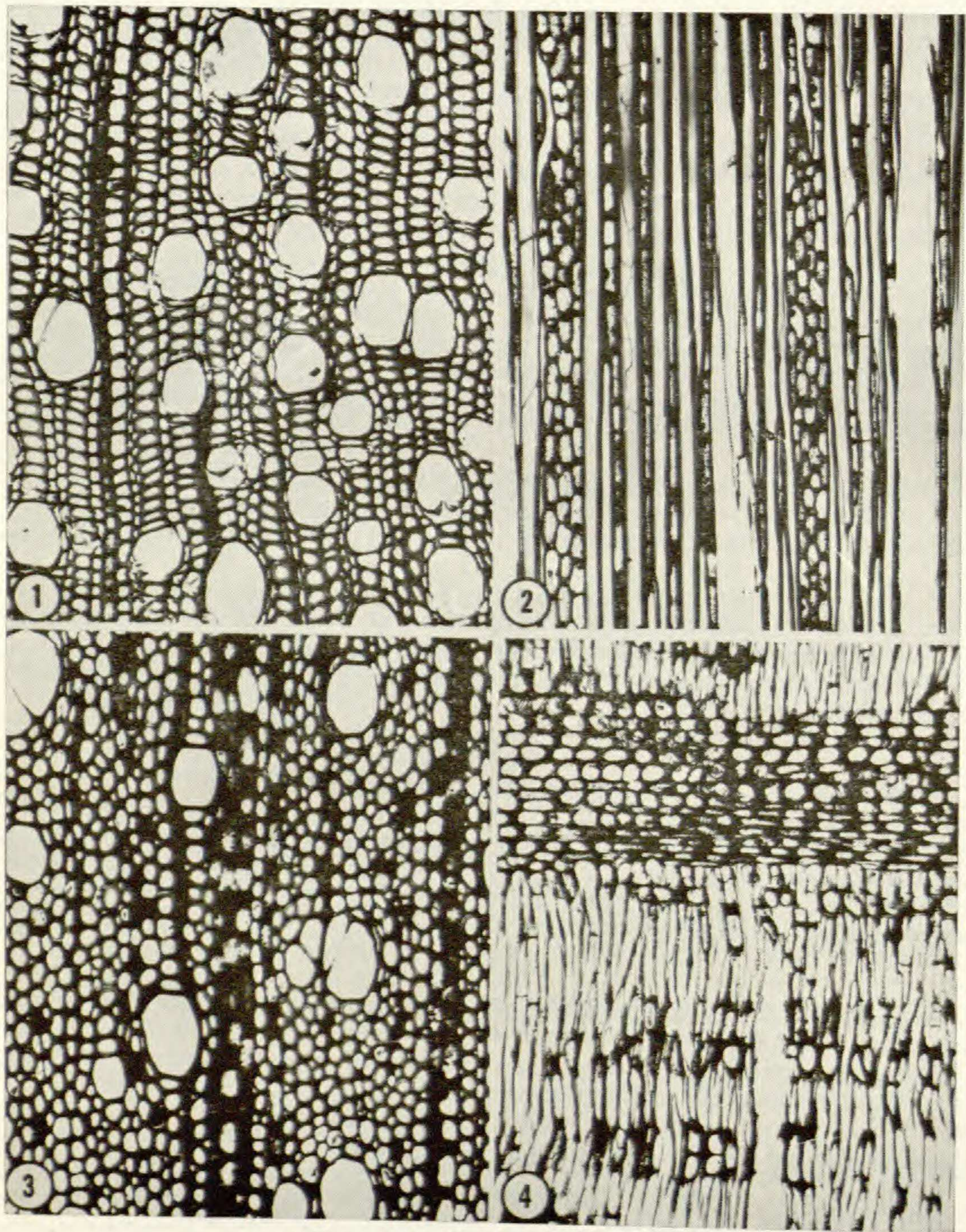
FIGS. 14-17. 14, *Curatella americana* L., cross section of wood showing solitary vessels, broad rays, aggregate to narrow-banded and paratracheal parenchyma, $\times 55$. 15, *Davilla rugosa* Poir., cross section of wood showing very large circular vessels and broad rays, $\times 55$. 16, *Curatella americana*, tangential section of wood, $\times 130$. 17, the same, radial section illustrating obliquely oriented, simple perforation plate, $\times 400$.

PLATE V

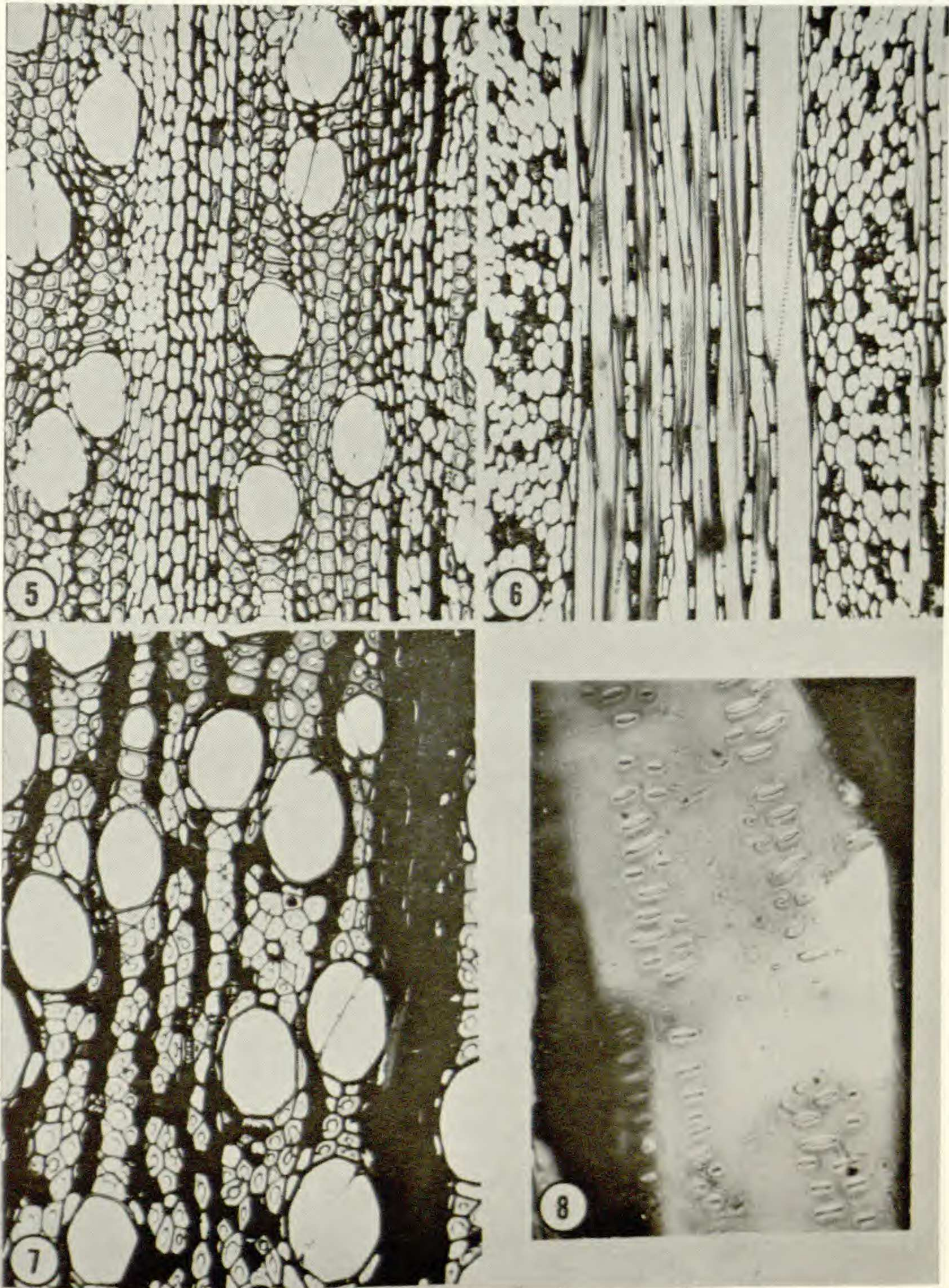
FIGS. 18-21. 18, *Tetracera volubilis* L., cross section of wood showing solitary pores and broad rays containing dark gummy deposits, $\times 60$. 19, *T. boiviniana* Baill., cross section of wood depicting a multiperforate perforation plate, $\times 400$. 20, the same, tangential section showing uniseriate and multiseriate rays, $\times 130$. 21, *Doliocarpus* sp., longitudinal section of wood showing opposite to transitional intervacular pitting with very elongate pits, $\times 400$.

PLATE VI

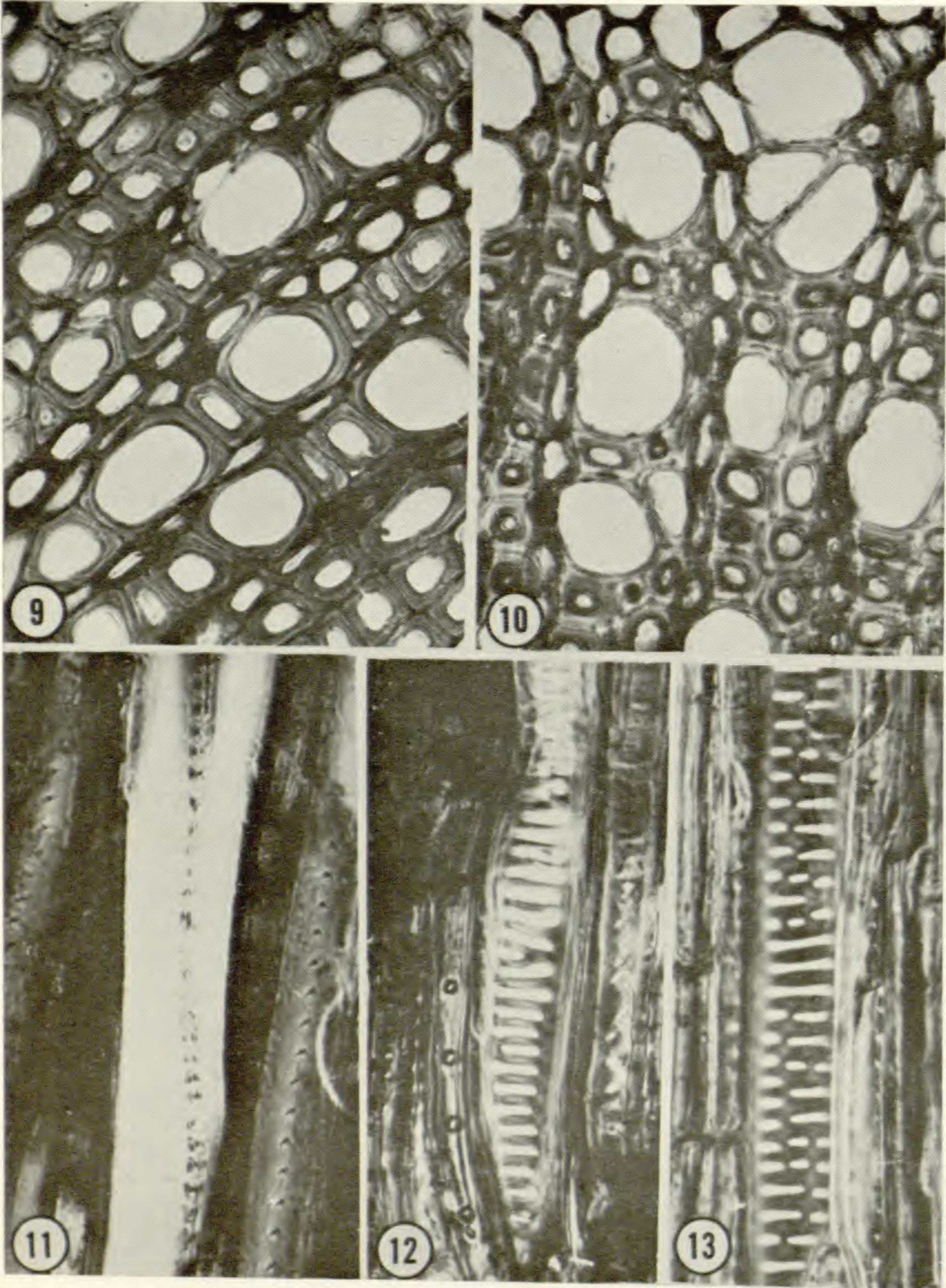
FIGS. 22-27. Vessel Member types in Dilleniaceae. 22, *Schumacheria castaneifolia* Vahl, $\times 400$. 23, *Dillenia triquetra* (Rottb.) Gilg, $\times 400$. 24, *Dillenia ingens* (B. L. Burtt) A. C. Smith, $\times 400$. 25, *Davilla aspera* (Aubl.) Benoist, $\times 400$. 26, *Doliocarpus dentatus* (Aubl.) Standl., $\times 400$. 27, *Tetracera volubilis* L., $\times 400$.



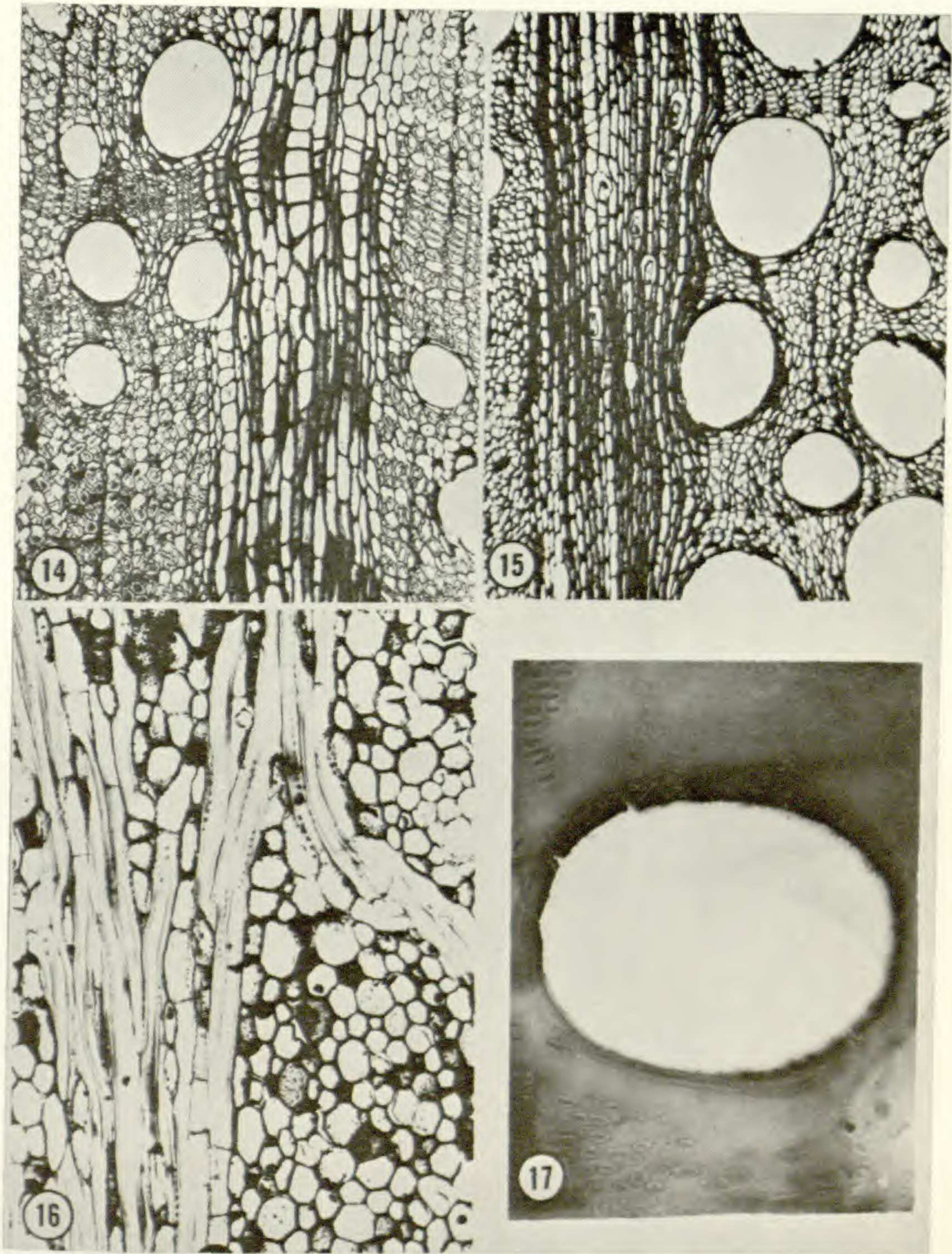
DICKISON, DILLENACEAE, I



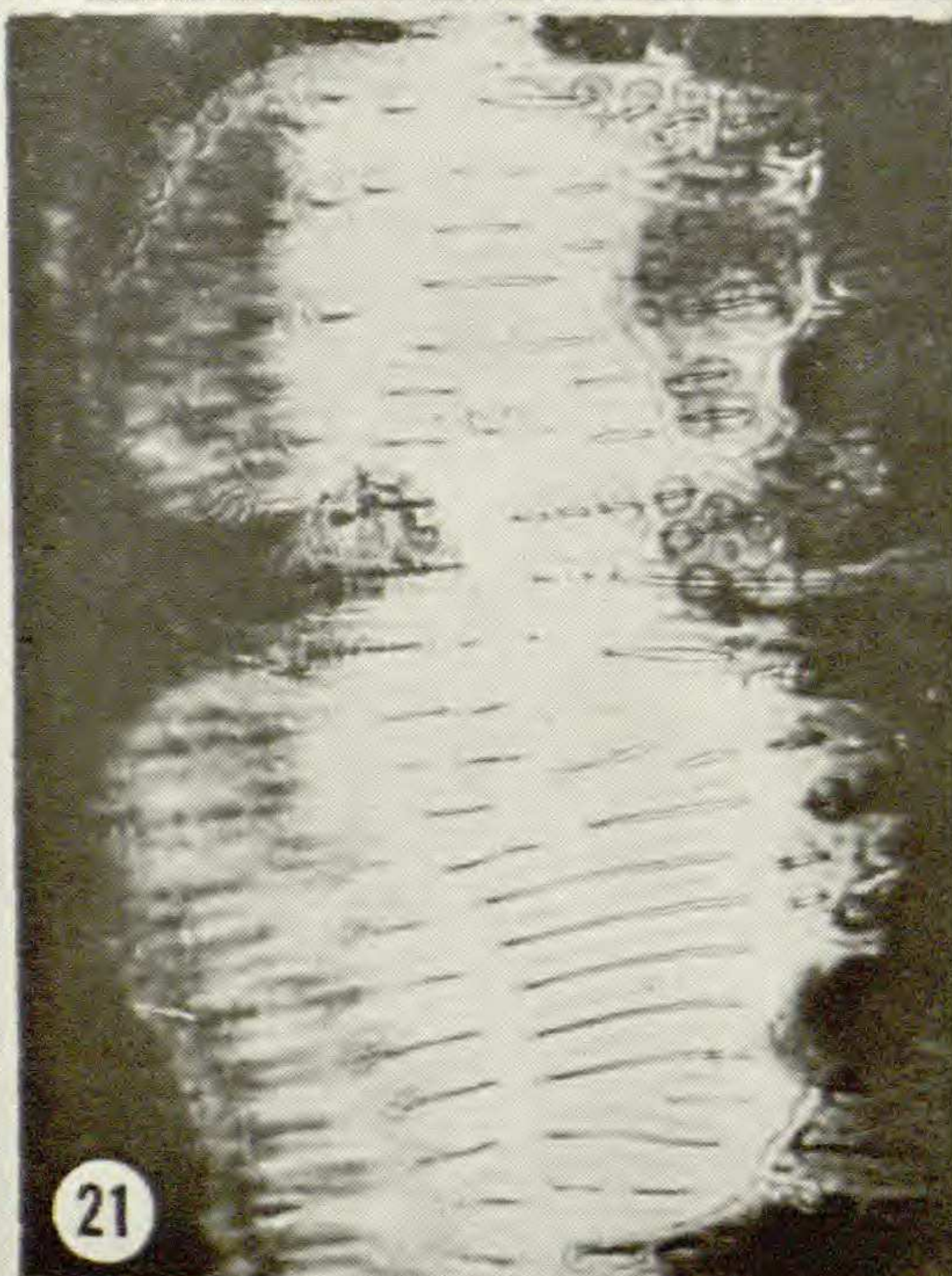
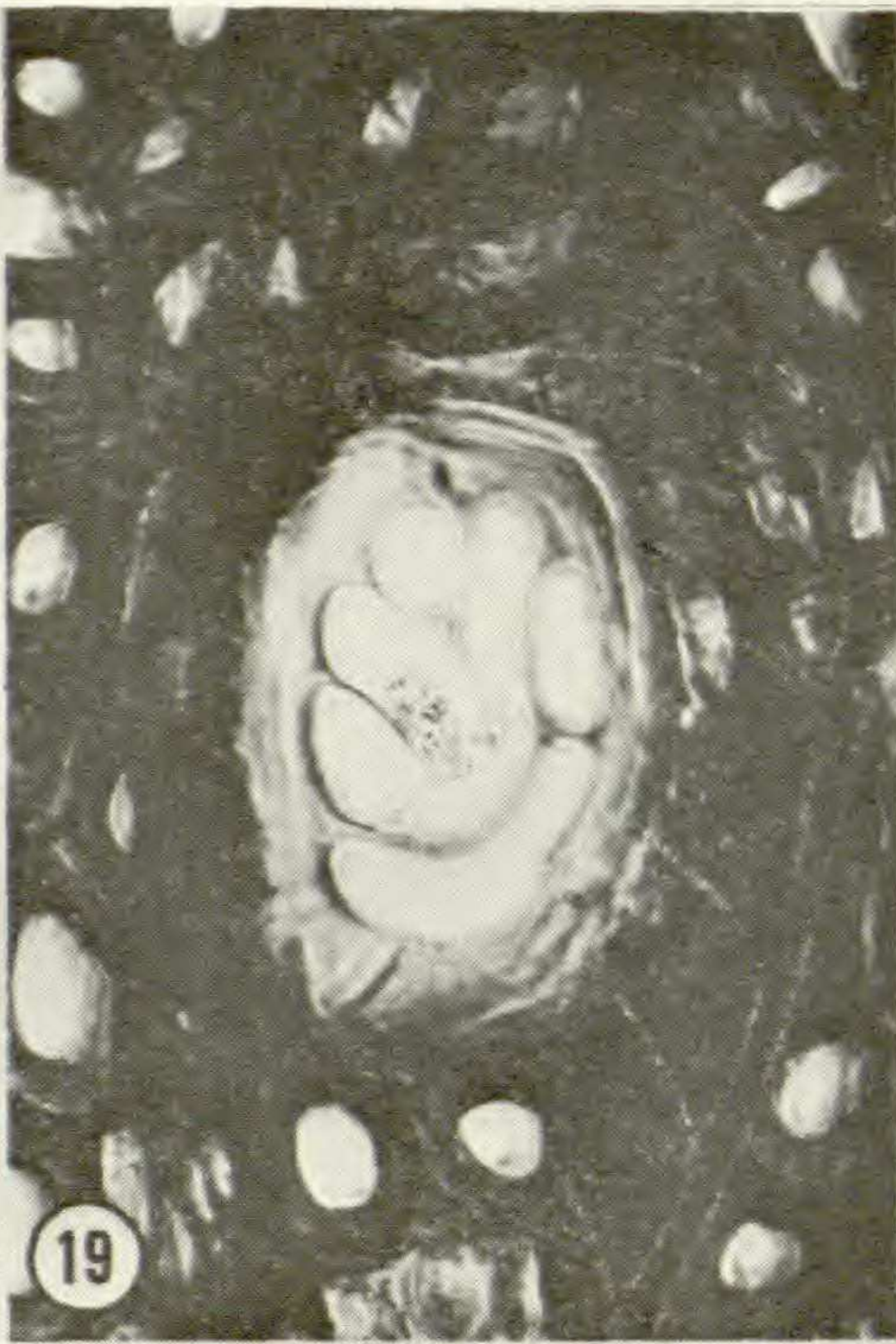
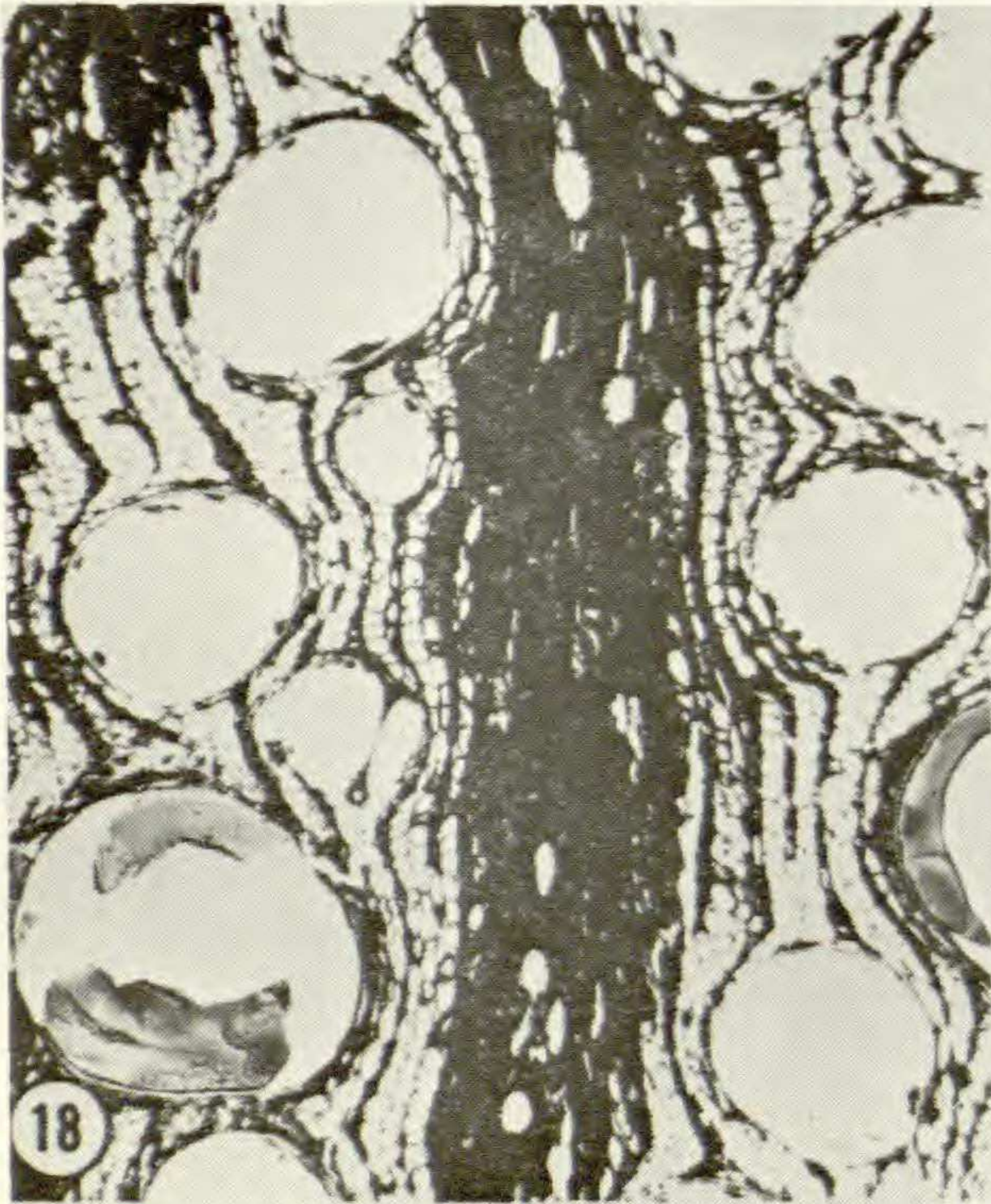
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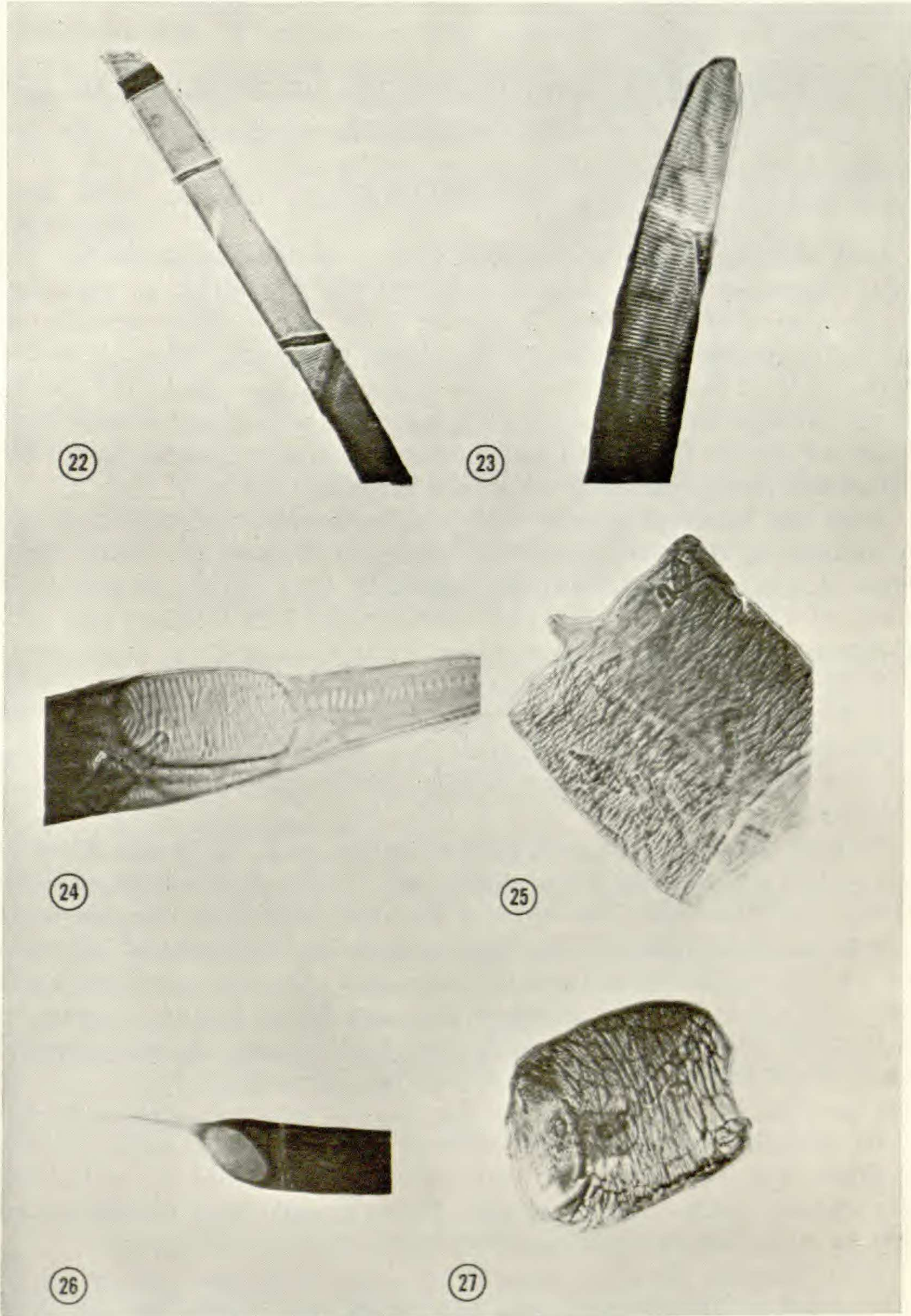
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